COMPARATIVE EMBRYOLOGY OF FOUR STANDARD VARIETIES OF *TRITICUM VULGARE* L.

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COMPARATIVE EMBRYOLOGY OF FOUR STANDARD VARIETIES OF TRITICUM VULGARE L.

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INTRODUCTION

One important aim in botanical science in recent years is to explain how the specific organization in plants is derived. Some investigations have been concerned primarily with the kernel or caryopsis, while others may have required extensive prerequisite knowledge of the developmental morphology of the individual organism.

These studies begin with the investigations of zygotic constitution and development and the assumption of form and structure in the individual plant with the influence of genetic, physiological, intra-physical and external environmental factors.

The purpose of the present study is to establish knowledge of the developmental morphology of the wheat embryo, not only the manner of development, but also the order and rate of development of tissue systems and organs in four standard varieties of hard red winter wheat.

Such a study of normal comparative development in the embryo would serve as a starting point for investigations of malformation of various kernel types in numerous other varieties and in abnormal genetic strains of wheat and wheat grass hybrids.

It is hoped that this investigation might lead to a better understanding of wheat embryogeny and its relationship to other ontogenetic features of the caryopsis.

REVIEW OF THE LITERATURE

The gross morphology of the embryo in grasses has been studied for over a century. The scutellum, coleoptile, epiblast and coleorhiza have been studied as special categories. The homologies of these organs have been the subject of most discussions and investigations.

Johansen (14)[1] Maheshari (17), and Wardlaw (30) refer to Souèges work on Poa annua L. as indicating a fairly regular and representative type for the Gramineae. In other genera, the cell differentiation patterns may be considerably less regular.

Artschwager and McGuire (2) in their studies of reproduction in Sorghum vugare L. presented evidence of a conspicuous antipodal complex which was assumed to be more or less common to all grasses. The precocious development of antipodals as compared to endosperm growth and the nucellar tissue was observed to persist as late as five days after fertilization.

Several morphologists have studied fertilization and organization in the Gramineae, beginning with anthesis and proceeding with the development of the embryo proper.

Sass (26) has reviewed Randolph's (23) work on fertilization in Zea mays L.

Brown (11) noted fertilization occurring in Avena sativa L. thirty

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[1] Figures in parenthesis refer to Literature Cited, page 24.

minutes after pollination. Morrison (20) set six hours after anther dehiscence for fertilization in some wheat ovules. Wakakuwa (29) stated that within fifteen hours after pollination, fertilization had occurred and that most fertilized eggs were in early prophase. Percival (22) observed fusion of the male gamete with the female gamete between thirty and forty hours after pollination. Artschwager and McGuire (2) referred to Stephens and Quinby's work with fertilization. They found fertilization to occur eight to ten hours after pollination in Sorghum vulgare L.

The organogeny of the embryo has been studied in several representatives of the grass family. Randolph (23) has shown the general cell shape of the zygote and the two celled stage in corn. The small terminal cell was described as lens-shaped. He described it as dividing vertically or obliquely, the later type of division leading to a temporary apical cell. The subsequent divisions were described as irregular. The embryo became clavate, narrow at the suspensor end and showed a gradient of smaller cells in the terminal growing region.

In comparative studies of the embryo in Avena sativa L., Zea mays L. and Triticum vulgare L., Avery (3) concluded that the homologies of the ventral scales, scutellums and coleoptiles were similar. Avery's illustrations show the mature embryo of Zea with five vegetative leaves covered by the coleoptile, Avena with two, and Triticum with three or four.

In Triticum vulgare L. McCall (16) considered that organogeny could best be understood by comparisons of relationships of organs and tissues in the mature plants.

Randolph (23) showed a rapidly enlarging pear-shaped embryo-sac in

the nucellar tissue and the small linear proembryo lying obliquely on the anterior side of the ovary. The proembryo was described as a clavate-shaped structure after enlargement with well defined cells of different gradation. The proembryo was largely an undifferentiated club-shaped structure up to the seventh day following fertilization. The eighth day changes were rapid and the differentiation of a tunicate layer of cells was formed over the distal region and extended down and over the suspensor. These peripheral cells divided both anticlinally and periclinally. The corpus cells divided in irregular planes. Growth was more rapid in the distal lobe and a zone of cells in a lateral position on the anterior side of the proembryo gave rise to the anterior lobe of the scutellum. The rapid enlargement and differentiation on the upper posterior side of the embryo resulted in the initiation of the plumule axis. The suspensor region ceased growth soon after the differentiation of the radicle and it persisted for a short time as a vestigial organ. The coleoptile was first observed as a small ridge of cells that developed around the shoot apex. The first vegetative leaf was initiated as a single ridge of tissue on the opposite side of the apical meristem. The apex eventually produced three to five additional leaf primorida.

Due to the present status of auxin studies, the coleoptile has received special emphasis and has been re-interpreted by many different authors: Randolph (23), Sargant and Arber (25), Merry (19), Percival (22), and Avery (3). Previous morphological studies of the embryo in Triticum vulgare L. do not present a precise understanding of the cytomorphogenesis of the earlier stages of development. Wakakuwa (29) made a study of morphological development in reciprocal crosses of interspecific hybrids of Triticum. In this study, he referred to Sax (1918)

as being the first investigator to demonstrate double fertilization in wheat. Wakakuwa's studies were based on interspecific crosses between T. spelta L., T. polonicum L. and T. aegilopoides L. The development following syngamy and endosperm formation was presented by the author in successive stages of development.

Morphological comparisons have been made of comparative embryo development in many inbred and hybrid crosses in the Gramineae by Fairchild (13), Martin (18), Naragunaswami (21), Stein (27) and Kennedy (15).

MATERIALS AND METHODS

The plant materials for this study were obtained from standard varieties of wheat grown under ordinary field conditions at the Oklahome Agricultural Experiment Station, Stillwater, Oklahoma.

Four standard varieties were selected as the basis of the present study because of their use in the wheat breeding program. The varieties, cereal identification numbers and chromosome numbers are shown in Table I.

TABLE I

FOUR STANDARD VARIETIES OF TRITICUM VULGARE L., AND THEIR CEREAL IDENTIFICATION NUMBERS

Variety	Cereal Identification Number*
Concho	12517
Comanche	11673
Blackhull	6251
Pawnee	11669

*Accession numbers are those of the Division of Cereal Crops, United States Department of Agriculture.

Field investigations of the growth rate of inflorescences were determined, and prior to fertilization, plants of approximately the same maturity were tagged for future selection. This method permitted random selection among uniform age groups in the four varieties.

Two spikes per variety were collected at intervals of approximately three days. Inflorescences were collected almost entirely between 1:00 and 3:00 a. m., promptly brought to the laboratory where the ovaries were excised, killed and fixed in a Craf III formula.

The ovaries were dissected in a mesipital manner, e.g. beginning at the center of the spike and collecting ovaries in both directions. This method was an aid in collecting older ovaries as well as younger ovaries in either direction from the central position in the inflorescence in each sample.

At least six ovaries were collected from each spike in this manner in order to obtain an adequate range in size and age. Ovaries selected after the period of starch deposition were first placed in a solution of 2% sodium sulphite and 2% lactic acid to soften the starch granules which were beginning to form in large numbers and to become hardened. These starch granules caused tremendous damage to sections during the microtoming operation and were difficult to handle. Material for microscopic study was processed in a Dioxan-n-butyl alcohol dehydration series and embedded in paraffin. The addition of stain to the series aided in the selection of sagital sections.

Paraffin sections 10 to 12 microns thick, depending upon the age of the caryopsis, were prepared and stained with a modified Flemming's Triple Stain for visual study and photomicrography.

Morphological Description of Varieties

Blackhull: Plant winter habit, midseason, midtall; stem white, midstrong; spike awned, fusiform, middense, inclined; glumes glabrous, white, usually with black stripes, midlong, midwide; shoulders wanting

to narrow, oblique; beaks 1 to 3 mm. long; awns 3 to 8 cm. long, sometimes black; kernels red, midlong, semihard to hard, usually elliptical; germ small to midsized; crease narrow, shallow; cheeks rounded; brush midsized, midlong, after Bayles and Clark (4).

Comanche: Plant winter habit, early to midseason, short to midtall; stem white, midstrong; spike awned, oblong, middense, inclined; glumes glabrous, white, short to midlong, midwide; shoulders narrow, wanting to elevated; beaks narrow, acuminate, 5 to 15 mm. long; awns 3 to 8 cm. long; kernels red, short to midlong, hard, ovate; germ midsized; crease midwide, middeep to deep; cheeks angular; brush midsized, midlong, after Bayles and Clark (4).

Pawnee: Plant winter habit, early, short; stem white, strong; spike awned, fusiform, middense, erect; glumes glabrous, white, short midwide; shoulders narrow to wanting; beaks narrow, acuminate, 3 to 5 mm. long; awns 3 to 8 cm. long; kernels red, short hard, ovate; germ midsized to large; crease midwide, middeep; cheeks rounded; brush small, midlong, after Bayles and Clark (4).

Concho: Plant winter habit, medium early, short to midtall, stem white midstrong, spike awned, lax, fusiform, medium to large. Spike awned. Middense, inclined; glumes glabrous, bronze to brown, short to midlong, midwide; shoulders narrow, wanting to elevated; beaks narrow, acuminate, 5 to 15 mm. long; awns 3 to 5 cm. long; kernel red, short to midlong, plump; germ midsized; crease midwide, middeep to deep; cheeks angular; brush midsized, midlong[42].

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[42]Oral Communication by Dr. A. M. Schlehuber, Small Grains, Agronomy Department, Oklahoma State University.

RESULTS

Organization of the Mature Embryo Sac

At the time of fertilization the ovule is about 1 mm. long. It is narrow radially and broad in the dorsivential plane. The embryo sac is somewhat pear-shaped, with the broader end nearest the micropyle. The young egg cell is globular to spherical. (Figure 4). As it increases in size it becomes balloon-shaped. Morrison (20) refers to the egg cell as being easy to identify due to small shiny bodies (fat globules). The nucleus is large and near the center of the cell. The cytoplasm is somewhat vacuolated and dense.

The synergids stand out as pear-shaped, to elongate, or tear-shaped. Sometimes they appear to be attached at some distance from the micropyle by a thin cytoplasmic strand. The cytoplasm is dense and alveolar; the nuclei are large and have prominent nucleoli. In some mature embryo sacs the synergids appear to shrink as the egg cell increases in size. (Figure 25).

The polar nuclei are usually found in close proximity to the egg cell. Both polar nuclei stand out as two complete cells with distinct cytoplasm. (Figure 25). Fusion of the polar nuclei occurs just prior to fertilization or briefly afterward. Fusion of the polar nuclei was not often observed in all the materials analyzed. They are usually larger in size than the synergids.

An antipodal cell complex has been assumed to be common to the grasses. The migration of the polar nuclei to the center of the embryo

sac coincides with mitotic divisions of the antipodals which are located at the chalazal pole of the embryo sac. Nuclear division in the antipodals is followed by cytokinesis, which results in a network of antipodal tissue that completely fills the chalazal end of the embryo sac. As the embryo sac enlarges the antipodals increase in number and sometimes appear to be free floating cells within the embryo sac. (Figures 25 and 26).

Many antipodal cells appear to have as many as four nuclei. The nuclei are smaller than the egg cell nucleus. The cytoplasm of the antipodal cells is dense and it stains very intensely.

Degeneration of the synergid cells was noted about five days after fertilization. This is not common in Sorghum Artschwager and McGuire (2) in which the synergids are shown to degenerate prior to fertilization. Disorganization of the antipodals deviates from that of Sorghum also, the antipodal nuclei in Sorghum disorganizes prior to fertilization while in Triticum the antipodals may be found as prominent structures with nuclei five days after fertilization. As many as thirty-six antipodal cells have been counted crowded in the chalazal end of the embryo sac. The disorganization of the antipodal cells is gradual as the nuclei appear to dissolve away.

Fertilization

The sequence of events relating to the fertilization process in Triticum from the time of pollination to the initiation of embrogeny and endosperm development has been described by Wakakuwa (29), Percival (22), Morrison (20), Avery (3), and Brenchly (10). The morphological and cytological details of fertilization were outside the scope of this investigation, but the time factor in relation to syngamy and the

beginning of kernel development were carefully studied. The materials selected for this investigation were chosen at random from test plots and therefore anthesis and pollen germination were not studied in detail, but observed at each collection period. The pollen is thought to germinate almost immediately after it reaches the style. Microscopic examinations of ovaries collected in conjunction with anthesis showed the mature sperm nuclei entering the micropylar opening in the more mature ovules. (Figure 26).

Postfertilization Development

The newly fertilized egg contains two nucleoli, one larger than the other. Either fusion of the two nucleoli occurs or the dissolution of one occurs shortly after fertilization, for only one nucleolus is present when primary endosperm-development is initiated.

The zygote and the primary-endosperm nucleus do not divide immediately after fertilization; they undergo a brief rest period, which is usually shorter for the endosperm nucleus but may be of considerable duration for the zygote.

During the rest period, general growth processes in the embryo sac and elsewhere in the ovule are continued.

A filiform apparatus appears in Triticum, as it also does in Sorghum, spreading out in a fan-like structure and coincident with the disintegration of the synergids. Since the nuclei may degenerate in the antipodals, the cells do not continue to enlarge but their walls thicken appreciably. They remain near the chalazal end of the embryo sac. As the endosperm develops the antipodals are crowded out into the disintegrating nucellus. They usually disappear before the endosperm reaches the distal end of the embryo sac.

Each variety was carefully analyzed and studied for the initiation and orientation of organ categories. Interpretations were made through developmental histology. (Table II).

The dates of collections were predetermined to establish patterns of development for this geographical area. Fertilization was established in each variety and the periodic collections were expressed in days after fertilization. A histology code was devised and used to derive a median stage of morphological development within each varietal collection. Each collection was uniform as to sample.

Each periodic collection, for each variety, was analyzed for one of the twenty-eight morphological characters assigned. The characters were arbitrarily selected.

Zygotic Division

The first division of the zygote is transverse. The cell divides into two equally distinct cells. The terminal cell is dome-shaped while the basal cell tapers to a point on the distal end. Thence the basal cell divides by a transverse division. Thus the initial divisions of the zygote are basipital in order of cell division. The fourth division occurs in the terminal cell and the new wall is vertical.

A zygote is present in each of the four varieties within a three day interval between May 9 and May 12. (Table II). The first division of the zygote occurs within two days after fertilization in all four varieties. A distinct elongation of the zygote occurs previous to the first division giving the zygote a balloon shape. (Figure 8).

TABLE II

COMPARATIVE DEVELOPMENT OF FOUR STANDARD VARIETIES OF TRITICUM

Days After Fertilization	Collecting Dates	Developmental Range				Histology Code
		Concho	Comanche	Blackhull	Pawnee	
	May 9	2	1	1	1, 2 A	1. Mature embryo-sac
	12	3, 7 A	1, 2, 7, 10 A	1	2, 3 A	2. Fertilization 3. Zygote elongation 4. Zygote division 5. 4 Cell stage
2	14	8, B	7, 10, 1 B	5, 4, 6 A	7, B	6. 8 Cell stage 7. 16 Cell stage
5	17	8, 9, 10 B	8, 10, 9, 16 B	8, 9, B	8, B	8. 32 Cell stage 9. Protunicate layer
7	19	8, 9, 10, 11, 23	9, 8, B	10, 11	9, 10	10. Coleoptile initials 11. Coleoptile groove 12. Radicle initials
9	21	14, 18, 15, 12 C	14, 23, 11, 15, 12 C	8, 14, 15, 18, 12 C	23, 13, 11, 12 C	13. Scutellar initials 14. Scutellum enlongation 15. Epiblast 16. Ventral scale
12	24	17, 19, 12C	12, 15, 18, 22 C	14, 20, 22, 17, 15 C	14, 15, 16, 22, 17 C	17. Seminal roots 18. 1st Foliage leaf 19. 2nd Foliage leaf
14	26	17, 22, 16	22, 24, 14, 19, 16	24, 14, 16, 22, 20	24, 22, 20	20. 3rd Foliage leaf 21. 4th Foliage leaf 22. Vascular traces
17	29	24, 22	17	17, 14, 21, 22	21, 25	23. Posterior lobe 24. Mature radicle 25. Mature embryo
20	June 1	21, 25	21, 25	20, 22		A. Free endosperm
22	2			21, 25		B. Endosperm cell walls C. Starch deposition

Proembryony

The morphological development of the proembryo in wheat is not well understood. The two to four day proembryo undergoes expansion by mitotic divisions which produces a small cellular clavate structure. (Figure 10).

This clavate-shaped proembryo soon elongates and pushes its way up into the newly formed endosperm tissue. (Figure 9). The proembryo develops a distinct layer of protunicate cells within five days after fertilization. (Figure 22). These cells are elongate and one cell layer in thickness. This layer covers the terminal dome and extends down over the suspensor completely surrounding the proembryo. The protunica divides anticlinally, giving rise to a continuous tunicate layer. The inner procorpus cells are more isodiametric in shape and divide in random planes.

Scutellar Initiation and Coleoptile Initiation

Many five day proembryos begin to develop a prominent bulge on the anterior side. The bulge is first noticeable as a meristematic zone of heavily stained cells in section, in the area of initiation. (Figures 15 and 16). The underlying corpus cells divide rapidly near the bulge and appear to be crowded together in a small area adjacent to the tunica layer. The tunica layer becomes extended by the internal cell divisions and a small primordium becomes apparent. (Figure 22).

The proembryo slows in its enlargement after the coleoptile primordium is initiated.

Samples collected seven to eight days after fertilization show histogen activities within the annular primordium of the coleoptile. This zonal activity produces the shoot apex primordium which gradually incre-

ases in size. A portion of this zone becomes the first foliage leaf. Leaf initiation is discussed in a later subsection. (Figure 13).

The scutellum is initiated in the distal end of the proembryo within nine days after fertilization in all varieties. (Table II). The scutellar primordium is first evident as a zone of darkly stained cells which undergo rapid meristematic division. This primordium is above and adjacent to the annular meristem of the coleoptile.

The protunicate layer differentiates a prominent distal peak, and the meristematic differentiation continues to form a scutellar plate which has a peripheral meristem. The scutellar primordium grows rapidly and the lateral margins fold in toward the anterior side, eventually partially enwrapping the embryonic root-shoot axis.

Radicle Initiation

The suspensor region probably serves the embryo as a nutritive and anchorage tissue. It may act as an area for the transfer of nutrient materials, however, this function has not been demonstrated other than the observation of differential staining effects and the tendency for the suspensor cells to become more vacuolate. At the time of scutellar initiation a meristematic zone in the central region of the posterior lobe, begins to develop. A saucer-shaped layer of cells becomes evident and the initiation of the radicle follows. A cleavage line is evident very early. (Figure 27). The cells along this line are elongate and occupy the outermost cell layer of the newly formed radicle (dermatogen-periblem initials). A histogen zone comprised of calyptrogen, dermatogen, plerome, and periblem is formed. The cleavage line separates the radicle from the lower mass of the suspensor and it becomes the coleorhiza. (Figure 23).

Epiblast and Ventral Scale Initiation

The epiblast is present in all four varieties and is apparent nine to twelve days after fertilization. (Table II). This small vestigial outgrowth is a prominent organ and is initiated in the region of the coleoptile node below the coleoptile. (Figure 17). Its function is unknown.

The ventral scale appears in cross section as a small prominent extension just below the terminal apex of the scutellum. It is present in all four varieties fourteen days after fertilization and was observed in Pawnee twelve days after fertilization. (Table II).

Seminal Roots and Provascular Strands

Two lateral seminal roots are present at maturity in all four varieties. The seminal roots are initiated in a region below the coleoptile node and the endogenous primordia extend downward toward the region of the epiblast. Anastomizing vascular traces in the coleoptile node are continuous with those in the radicle and seminal roots. A prominent root cap is also present on the seminal root primordium as well as on the radicle. (Figure 23).

Provascular strands are evident in all varieties within twelve to fourteen days after fertilization. (Table II). They first appear in the region of the coleoptile node and extend up into the scutellum. As the coleoptile emerges and the foliage leaves are formed, vascular traces are differentiated in the new leaves before formancy occurs. The provascular strands elongate and undergo differentiation to form the permanent vascular tissue following germination of the seed. (Figure 17).

Initiation of Foliage Leaves

The foliage leaves are derived from meristematic divisions in the shoot apex simultaneously with coleoptile initiation. The corpus cells of the shoot apex divide rapidly and produce an annular ring of elongate cells on the shoot apex which produce the foliage leaf. New leaves are initiated in acropetal, distichous order on the shoot apex.

The first foliage leaf is initiated between the ninth and twelfth day after fertilization in all varieties. (Table II). The second foliage leaf was observed in Comanche at fourteen days, and in Concho at fifteen days after fertilization. The third foliage leaf is present in Blackhull and Pawnee fourteen days after fertilization. The fourth foliage leaf was not evident until seventeen to twenty days after fertilization in all four varieties. (Table II). The shoot apex contains four primordial foliage leaves in the mature embryo. Four foliage leaves are present in all the varieties studied.

The embryo of Concho and Comanche possess all the mature morphological characters shown in Table II within twenty days after fertilization.[13] (Figures 17 and 18). Several morphologically mature embryos were noted in Pawnee seventeen to twenty days after fertilization. (Figure 19). The mature morphological features did not become evident in Blackhull until twenty-two days after fertilization. (Figures 20 and Table II).

Endosperm and Starch Grain Formation

The endosperm begins to form immediately after fertilization with several successive divisions of the endosperm nucleus. At first a thin

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[13] Maturity characteristics are based upon the number of foliage leaves, vascular traces, radicle and seminal root development and endosperm composition.

cytoplasmic strand fills the embryo sac. This strand contains many free nuclei. The cytoplasm is more dense near the zygote and more free nuclei are adjacent to the zygote. As the zygote divides and differentiates into the proembryo the nucellar tissue rapidly breaks down and is replaced by the expanding free nucleate endosperm. (Figure 6). From two to five days after fertilization, the endosperm nuclei adjacent to the proembryo begins to differentiate and form cell walls. Within seven days, endosperm cell walls are evident throughout the rapidly expanding tissue. (Table II). (Figure 24). Starch granules were noted in the endosperm five days after fertilization and were observed to persist in large numbers up to seven days after fertilization. (Table II).

Abnormal Embryology

Only one abnormality was evident and clearly defined during this course of study. This abnormality was observed in a mature embryo of the Blackhull variety. The epiblast which normally may be appressed to the cotyledonary node or extending away at a small angle from the node, was found to be growing back into the region of the cotyledonary node as shown in Figure 21. This is a near median section and exhibits morphological characters otherwise normal in the mature embryo.

DISCUSSION

The fertilized egg cell divides transversely to form a two-celled proembryo. The basal cell divides again in a transverse plane. The third division takes place in the apical cell and is vertical.

Early embryogeny in Triticum has been described as basipital as observed in several grasses; Randolph (23), Abbe and Stein (1) Zea mays; Avery (3) Avena sativa; Artschwager and McGuire (2) Sorghum vulgare; Cannon (12) Avena fatua; and Wakakuwa (29), Percival (22), Morrison (20), and Redei (24) Triticum vulgare.

The young proembryo becomes clavate shaped in structure and remains clavate for a period of three to five days after fertilization.

In this study four varieties of hard red winter wheats were selected for comparison of histogen initiation and morphologically distinct characters. Each variety was compared in Table II by means of a morphological development range based upon histogen and organ initiation.

Fertilization for all four lines studied was observed to occur between May 9 and May 12. (Table II).

After a period of two days following fertilization, the first division of the zygote usually has occurred and the free endosperm nuclei are present in the embryo sac.

Morrison (20) has stated that there are from one to four cells present in the proembryo two days after fertilization. Brenchly (10) states that the first division does not occur until five days after pollination. Percival (22) described the divisions of the zygote to be from forty to

fifty hours after pollination and that they may possibly be due to atmospheric conditions and temperature. Wakakuwa (29) observed the two-celled proembryo at twenty-four hours after fertilization.

The free nuclei of the endosperm appear soon after fertiliztion as a prominent cytoplasmic halo almost completely surrounding the new zygote which grows out gradually into the nucellar tissue.

As the endosperm expands the nucellar tissue is gradually broken down and replaced by the thin line of cytoplasm with free nuclei of the newly formed endosperm. The endosperm nuclei are numerous nearest the zygote and may possess several nucleoli. Morrison (20) states that the free endosperm nuclei are mitotically synchronized to some degree, and that most free nuclei are always in the same stage of mitotic division. A careful analysis of endosperm cells was not a part of this study, however most endosperm cells encountered in the earliest phases of development were in the same relative mitotic stages. The transitional phase from the milk stage to starch formation with the addition in mass of the endosperm cell walls and thick starch granules is relatively the same as that proposed by Bradbury, Cull and McMasters (7,8) in studies analyzing the baking and milling quality of hard red winter wheats.

The starch granules appear within five to seven days after fertilization. (Table II). The starch granules become larger and eventually fill the isodiametric endosperm cells and squeeze the endosperm nucleus into a small star-shaped structure occupying a small position in the cell. Bradbury, Cull, and McMasters (6,7,8,9), Thompson (28) and Bessey (5).

The proembryo remains as a relatively undifferentiated clavate structure up to the seventh day following fertilization which is in agreement with Randolph's (23) study on Zea; Wakakuwa's (29) and Percival's

(22) analysis of wheat varieties.

The coleoptile is initiated from the upper anterior side of the clavate proembryo as a result of meristematic activity, within seven days after fertilization. (Table II). The plumule axis (shoot apex) develops rapidly initiating the floral organs in an acropetal, distichous order on the shoot apex, which results in the morphological development of four foliar leaves in all mature varieties studied.

The organogeny of the scutellum is well understood in Zea as described by Randolph (23) and appears to be initiated in a similar way in Triticum with one exception. In Zea the lateral margins of the scutellar primordium completely enclose the root shoot axis and may over lap. This morphological character is observed in cross-sections of Triticum as lateral margins folding inward enwrapping the root-shoot axis but not forming an embryonic enclosure. The distal lobe gives rise to a meristematic zone which elongates and produces a rudimentary cotyledon (scutellum = ?). The ventral scale is initiated near the terminal apex of the scutellum within twelve to fourteen days after fertilization in all four varieties. (Table II).

The radicle initials are evident as a saucer-shaped zone of meristematic cells near the base of the proembryo and are endogenous. It is initiated at the same approximate time as the scutellum.

Seminal roots are evident, near maturity, in the embryo and appear to be initiated from meristematic areas adjacent to the cotyledonary node.

Three seminal roots are evident in Zea Randolph (23) but only two lateral seminal roots are evident in Triticum at maturity.

The rapidly maturing embryo possesses vascular traces twelve days after fertilization in all four of the varieties compared. Vascular

traces are prominent in the mature foliage leaves and the scutellum in early initiation phases. The anastomising of vascular traces is evident in the cotyledonary node at maturity and join the radicle, seminal roots, scutellum, and foliage leaves.

SUMMARY

An embryological study by comparative methods was carried out on four standard varieties of hard red winter wheat. A histological account is given of the developing embryo.

Each variety was carefully analyzed for twenty-eight morphologically distinct features and they are presented in table form.

The histogen initials in the shoot and root apices are discussed. The organogeny of tissue systems is tabulated in terms of days after fertilization. The resulting conclusions are almost identical for development of organ categories and tissue systems in other related grasses (*Zea*, *Sorghum* and *Avena*).

Embryo maturity is reached in all four varieties within twenty-two days after fertilization. The varieties Concho, Comanche and Pawnee mature two to three days earlier than Blackhull. This information is substantiated by the analysis of each variety at field maturity.

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LEGEND FOR PLATE I

Fig. 1 Transverse section of terminal antipodal complex. (320X).

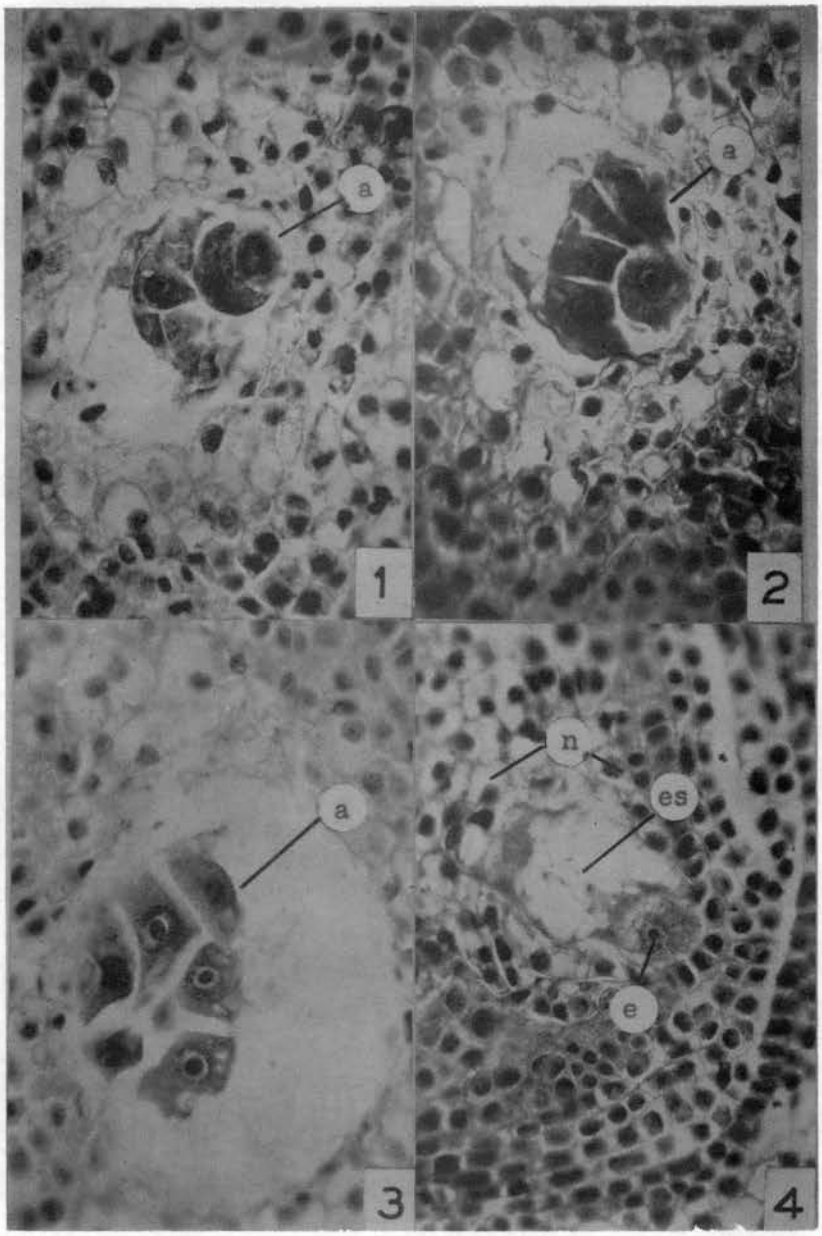
Fig. 2 Transverse section of antipodal complex sectioned at 10 microns below Fig. 1. (320X).

Fig. 3 Transverse section of antipodal complex sectioned at 10 microns below Fig. 2. (320X).

Fig. 4 Transverse section of the egg cell in position near the micropyle with surrounding nucellar tissue.

Antipodal complex (a); egg (e); nucellar tissue (n); embryo sac (es).

PLATE I



LEGEND FOR PLATE II

Fig. 5 Longitudinal section of the embryo sac of Blackhull with a zygote. (320X).

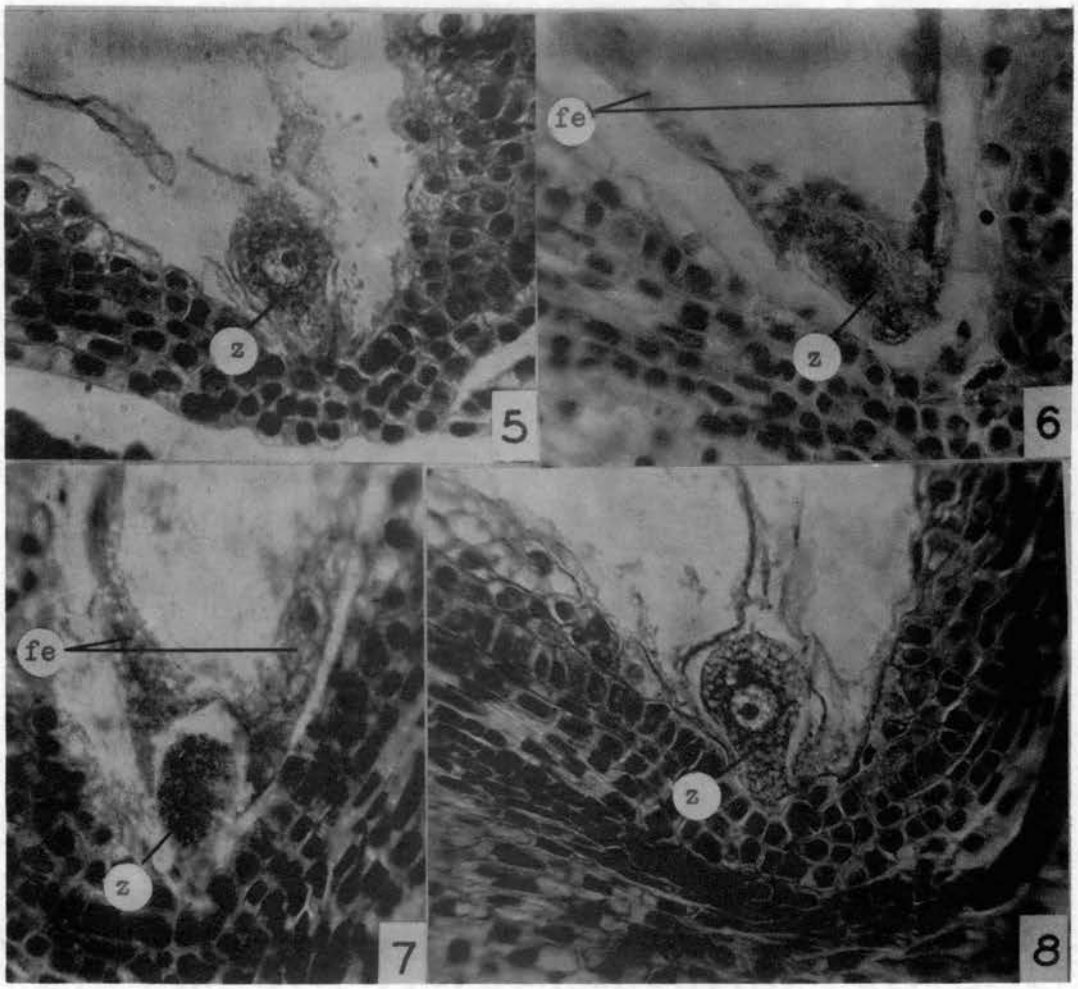
Fig. 6 Longitudinal section of the embryo sac of Concho with a zygote and free endosperm nuclei. (320X).

Fig. 7 Longitudinal section of the embryo sac of Comanche with a two-celled proembryo and free endosperm nuclei. (320X).

Fig. 8 Longitudinal section of the embryo sac of Pawnee with a zygote. Note that zygote possesses a projected suspensor connecting with the micropyle.

Zygote (z); free endosperm nuclei (fe).

PLATE II



LEGEND FOR PLATE III

Fig. 9 Longitudinal section of the proembryo of Pawnee with endosperm cell walls forming, five to seven days after fertilization. (74X).

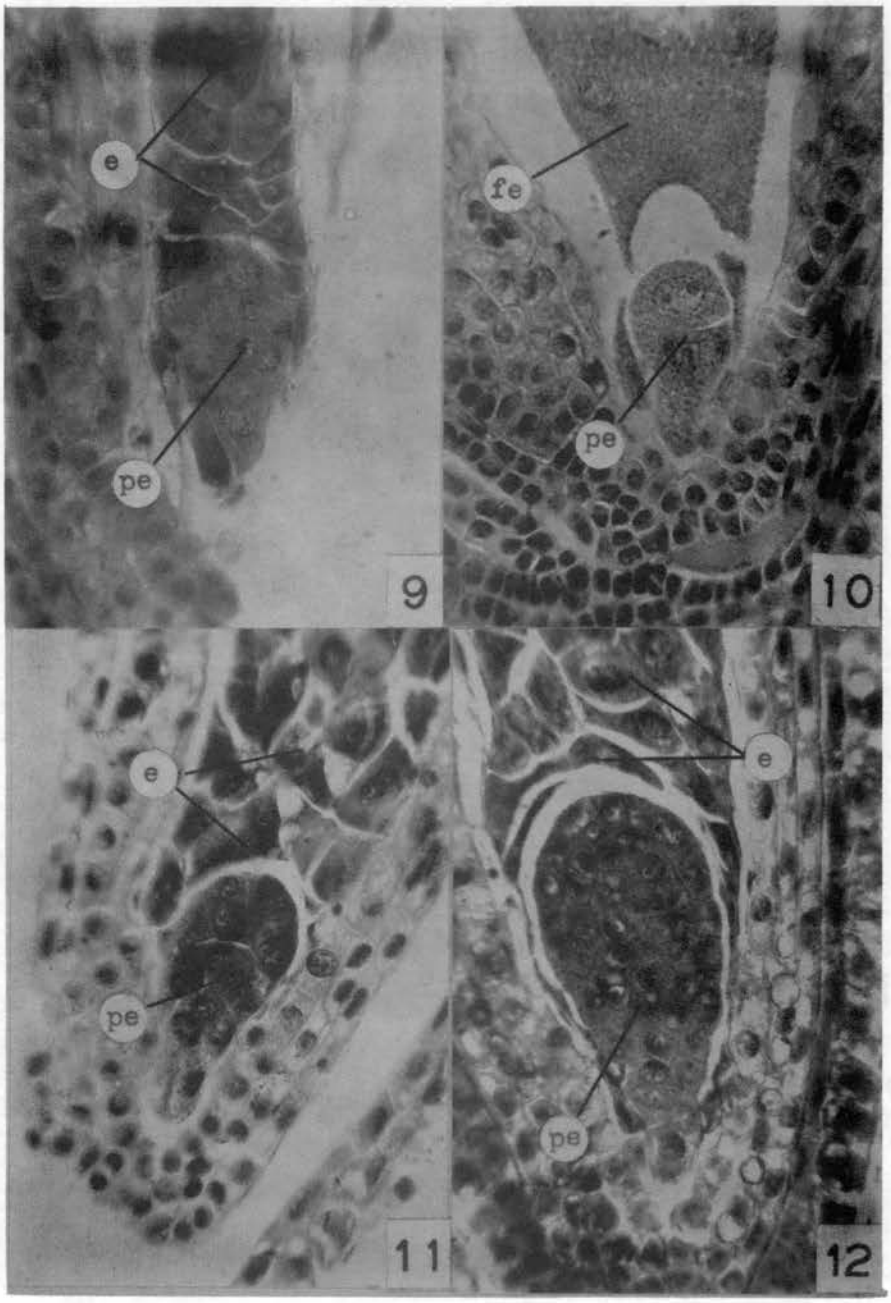
Fig. 10 Longitudinal section of the proembryo of Blackhull five days after fertilization. Note that free endosperm nuclei are evident at this stage. (74X).

Fig. 11 Longitudinal section of the proembryo of Concho with endosperm cell walls present. Five to seven days after fertilization. (74X).

Fig. 12 Longitudinal section of the proembryo of Comanche with endosperm cell walls present. Seven days after fertilization. (74X).

Free endosperm (fe); endosperm with cell walls (e); proembryo (pe).

PLATE III



LEGEND FOR PLATE IV

Fig. 13 Longitudinal section of embryo of Blackhull showing coleoptile and scutellum initiation. (74X).

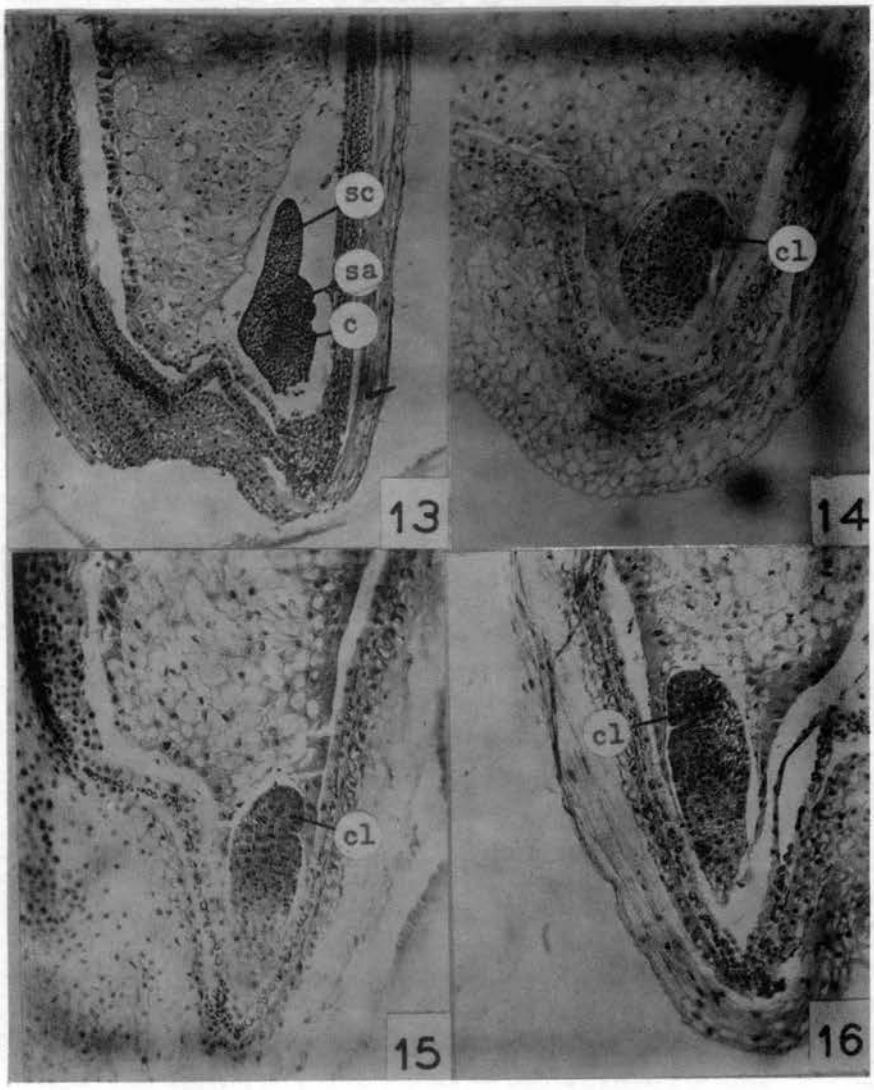
Fig. 14 Longitudinal section of proembryo of Comanche with initiation of coleoptile. (74X).

Fig. 15 Longitudinal section of proembryo of Blackhull showing elongation of supensor and meristematic zones and the initiation of coleoptile lip. (74X).

Fig. 16 Longitudinal section of proembryo of Concho showing elongation of suspensor and meristematic zones of initiation of coleoptile lip. (74X).

Coleoptile (c); scutellum (sc); coleoptile lip (cl); shoot apex (sa).

PLATE IV



LEGEND FOR PLATE V

Fig. 17 Longitudinal section of mature Concho embryo. (33X).

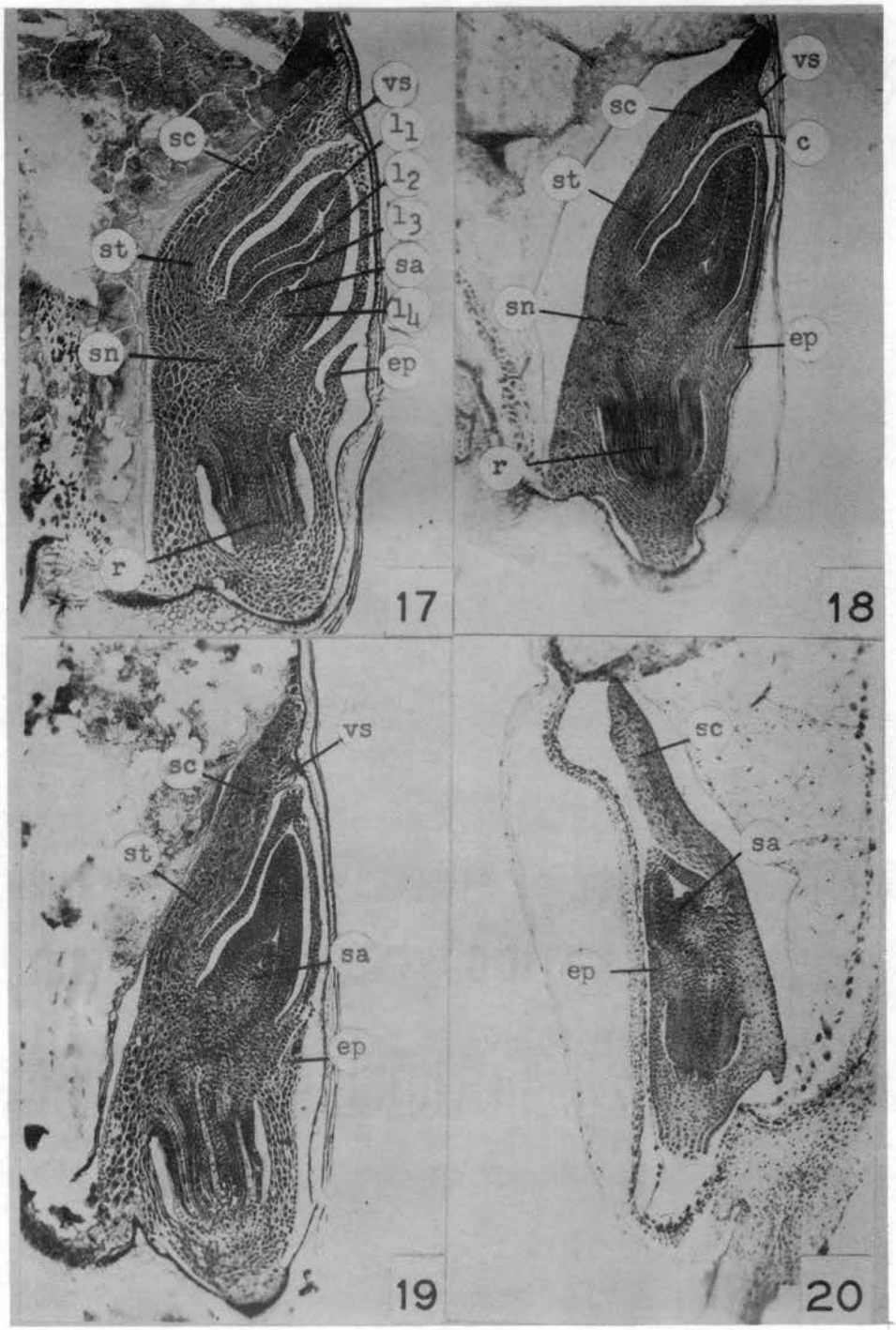
Fig. 18 Longitudinal section of mature Comanche embryo. (33X).

Fig. 19 Longitudinal section of mature Pawnee embryo. (33X).

Fib. 20 Longitudinal section of mature Blackhull embryo. (33X).

Scutellum (sc); coleoptile (c); epiblast (ep); ventral scale (vs); scutellar node (sn); radicle (r); scutellar traces (st); shoot apex (sa).

PLATE V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LEGEND FOR PLATE VI

Fig. 21 Longitudinal section of Blackhull embryo. The epiblast in this near median section is abnormal and is growing back into the region of the coleoptile node. (74X).

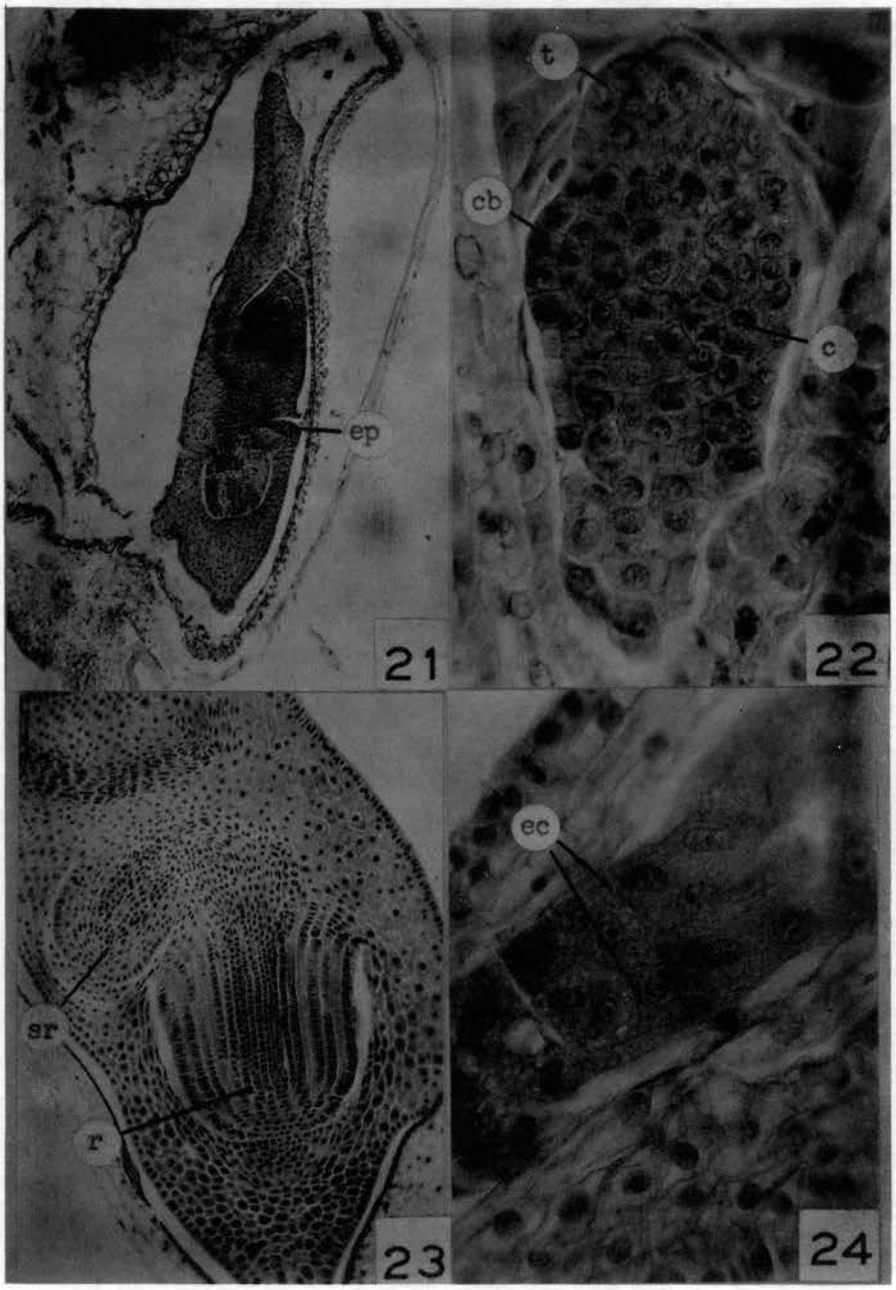
Fig. 22 Longitudinal section of proembryo with prominent coleoptile bulge. Note the one cell tunica layer surrounding the proembryo. (320X).

Fig. 23 Longitudinal section of embryo showing mature radicle and seminal root. (320X).

Fig. 24 Longitudinal section of endosperm cell development. Note cells nearest the micropyle and proembryo are first to derive cell walls. (320X).

Mature radicle (r); seminal root (sr); coleoptile bulge (cb); tunica (t); corpus (c); epiblast (ep); endosperm cells forming cell walls (ec).

PLATE VI



LEGEND FOR PLATE VII

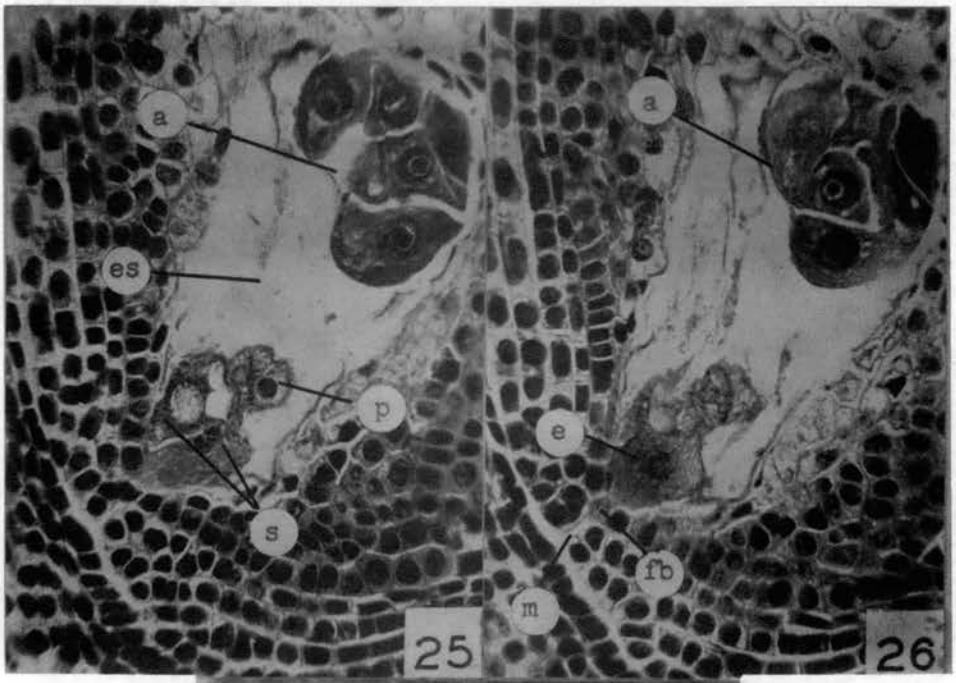
Fig. 25 Longitudinal section of embryo sac 10 microns below Fig. 26. Note large synergids antipodals and dark staining polar nuclei.

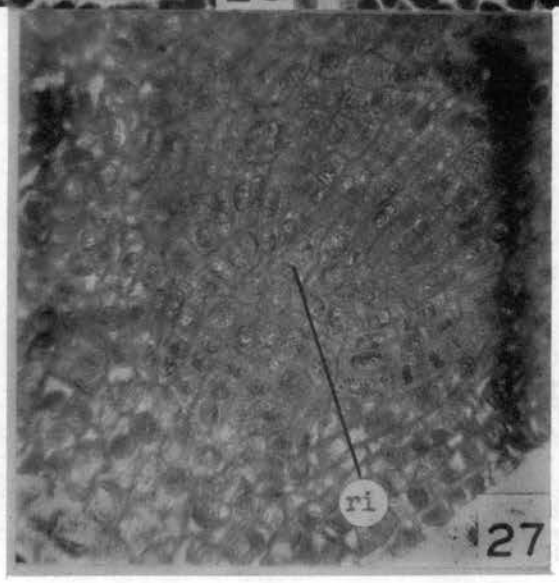
Fig. 26 Longitudinal section of embryo sac with egg and antipodal complex. A small fusion body is present in the micropyle. (320X).

Fig. 27. Longitudinal section of embryo showing radicle initials.

Egg (e); antipodals (a); synergids (s); polar bodies (p); micropyle (m); fusion body (fb); radicle initials (ri).

PLATE VII





LEGEND FOR PLATE VIII

Fig. 28 Longitudinal section of mature caryopsis of Concho. (X15).

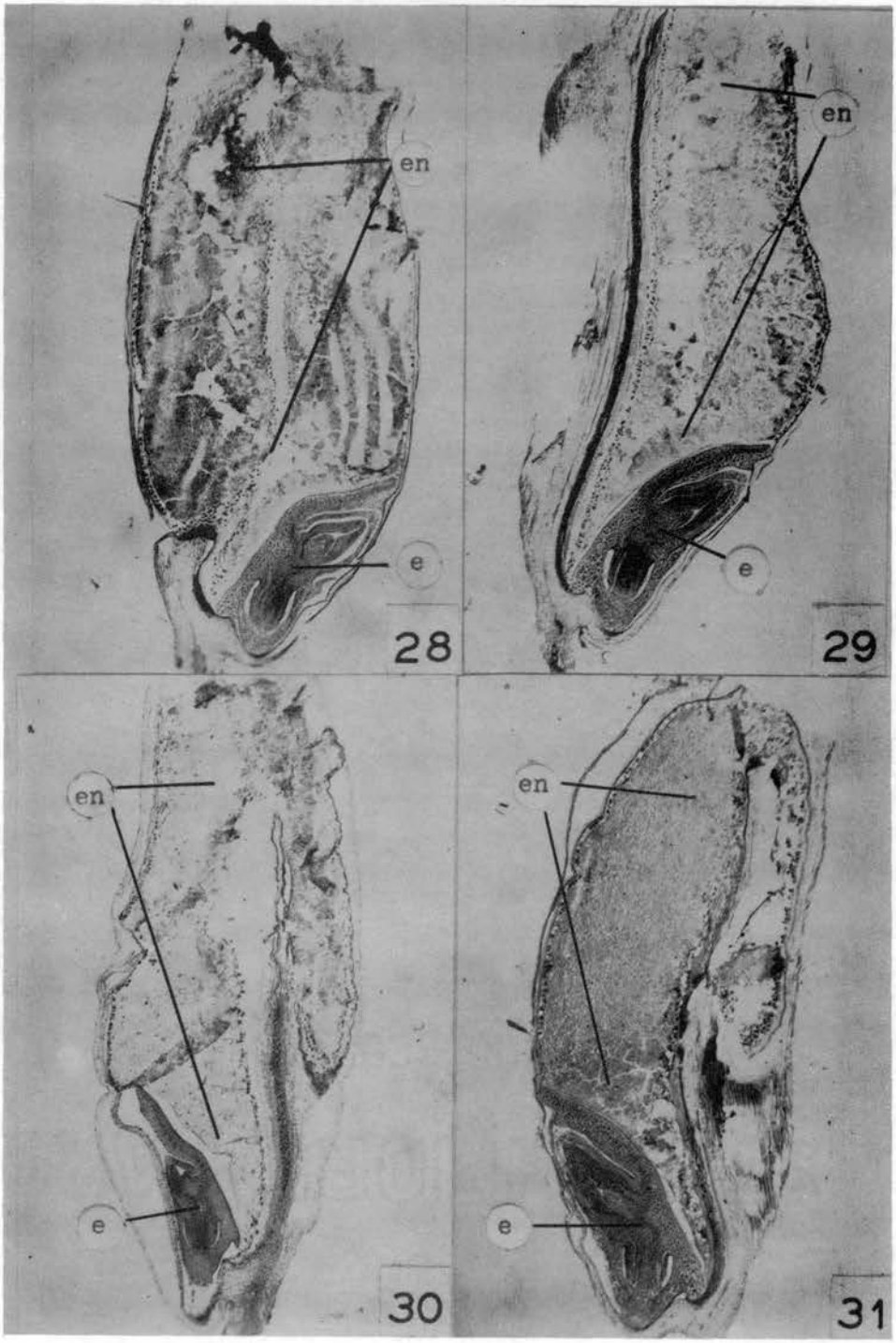
Fig. 29 Longitudinal section of mature caryopsis of Comanche. (X15).

Fig. 30 Longitudinal section of mature caryopsis of Blackhull. (X15).

Fig. 31 Longitudinal section of mature caryopsis of Pawnee. (X15).

Embryo (e); endosperm (en); pericarp (p).

PLATE VIII



VITA

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